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Population dynamics of *Musculus Senhousia* and *Protothaca* *Staminea* in Tomales Bay, California

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POPULATION DYNAMICS OF MUSCULUS SENHOUSIA
AND PROTOTHACA STAMINEA IN TOMALES BAY, CALIFORNIA

A Thesis

Presented to
the faculty of the Graduate School
University of the Pacific

In Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
David McClain Nelson

August 21, 1981

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ABSTRACT

The changes in population density, growth and biomass of two infaunal, sympatric, suspension-feeding bivalves, Musculus senhousia (Benson, 1842) and Protothaca staminea (Conrad, 1837), have been investigated over an eighteen month period in Tomales Bay, California. M. senhousia, a mussel, displays two basic spawning times, one of which occurs in late spring, while the second spawning takes place in late summer. P. staminea, a venerid, spawns once during late spring. The population density of the mussel ranged from $9,180 \text{ m}^{-2}$ in early spring to 752 m^{-2} in the fall of 1976. P. staminea had a maximum density of $1,120 \text{ m}^{-2}$ in the summer, and the minimum of 265 m^{-2} coincided with winter. The growth of M. senhousia appears to take place primarily during the spring and summer months, while that of P. staminea occurs in late winter and summer, with a slight recession during the spawning period. The Bertalanffy growth equation was applied to both species and it was found that M. senhousia grows to a shell length of approximately 25 mm in 10 to 11 years; whereas, P. staminea reaches a shell height of 37 mm in 15 to 16 years. There was a large seasonal variation in biomass of both species with the greatest difference occurring between winter and spring for the mussel, while that of the venerid took place immediately before and after spawning. Not only

were the older age groups better represented in the population of M. senhousia, but also the smaller sizes both experienced higher mortality and tended to predominate in the upper intertidal areas. The densest population of both species occurred between the tidal heights of 1.10 m to .28 m, which occupies the middle intertidal zone (MLW). The sediment in these areas ranged from coarse to medium sand.

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INTRODUCTION

In this study, seasonal changes in the abundance, distribution, recruitment, biomass and growth are reported for two suspension-feeding bivalves occurring together at the same locality in Tomales Bay, California. Various hypotheses concerning factors regulating the populations of intertidal suspension feeders have been proposed (Seed, 1969; Green, 1969; Green and Hobson, 1970; Levinton, 1972; Woodin, 1974) although comparatively few have been investigated.

The two bivalves studies are the venerid, Protothaca staminea (Conrad, 1937), and the mytilid, Musculus senhousia (Benson, 1842). Musculus senhousia is a fragile, thin-shelled bivalve common in Tomales Bay, California. Initially introduced from Japan prior to 1944, it now ranges from Washington to central California and eastern Asia (Hanna, 1954). M. senhousia exists infaunally in the upper substrate and has generally been found on mudflats in sheltered areas. Except for taxonomic description (Smith and Carlton, 1975), no literature on M. senhousia is available. Protothaca staminea is also an infaunal suspension feeder and occurs from the Aleutian Islands to Cape San Lucas, Baja California (Feder and Paul, 1975). The venerid commonly occurs in sandy substrate (Smith and Carlton, 1975). The site selected in Tomales Bay contained a wide enough range of substrate to accommodate both species.

MATERIALS AND METHODS

Tomales Bay is relatively sheltered. The shoreline consists of silty clay areas with sporadic coarse sediment patches (Daetwyler, 1966). A 250 m² transect was established in one of these patches, extending both above and below the two bivalve populations. The site selected was approximately 2 miles south of the town of Marshall on the east side of the bay (Figure 1).

The transect was subdivided into five areas of 5x10 m. The longer side paralleled the shore, and the areas were marked with permanent stakes. Stratified random samples were taken using replicate cores sampling 1/100 m² to a depth of 5 cm. Collections were taken between April, 1975 and September, 1976. It was found that both species did not live below 5 cm in the substrate.

The samples were sieved through a 1 mm screen, fixed in 5% seawater formalin, and subsequently preserved in 70% isopropanol. Measurements were taken of the length, width and height of both species according to the methods of Fraser and Smith (1928) and Rickets and Calvin (1968). The shell dimensions best representing growth for each species were employed. Total length and height were used for the mussel and venerid, respectively. Weighted means were derived and plotted from average dimensions of each age group. Additionally, for comparison, a length/height

regression was performed for P. staminea (Figure 17).

Biomass determinations were made from October, 1975 through September, 1976 from bivalve samples of the most abundant area. The bivalves were rinsed and placed in circulating seawater for 24 hours to purge them of sediment. Each specimen was then scrubbed, measured and weighed to determine the total wet weight. Dry tissue weight was determined using the methods of Gilbert (1973).

At each sampling time a 2 cm diameter x 5 cm deep sediment sample was collected randomly from each of the areas. Sediments were analyzed using the techniques of Folk and Ward (1957). Tidal heights of the stakes were surveyed for each area using the methods of Feder and Paul (1973). The height of each stake above the substrate was then measured monthly to monitor sediment height changes.

Temperatures were recorded between monthly collections using Taylor mini-max thermometers in areas I and IV, representing high and low tidal heights of the transect, respectively (Figure 2).

All statistical analyses were either performed on a Burroughs B6700 computer or an HP-97 calculator.

RESULTS

Musculus senhousia

Nine thousand and twenty bivalves were examined (Figures 3 and 4). Both monthly size-frequency fluctuations as well as biomass variations were noted. Abundance and size distribution changes are shown (Figures 3 and 4). Size distributions at different tidal levels are summarized for 4 representative months in Figure 5. July and October, 1975, represent typical months of growth while February and June show deviations, possibly due to winter stress and recruitment.

Rapid decline in abundance follows recruitment in the spring (Figure 3). Abundance then remains stable throughout the summer and fall, decreasing again in the winter. Spring recruitment is associated with size distributions that are skewed to small sizes (Figure 4) followed by a shift to larger sizes and subsequent stabilization in size distributions throughout the summer and fall. Larger M. senhousia occur in the lower intertidal areas except during spring recruitment (Figure 5). The majority of the population always occurred in areas II, III, and IV (Figure 6), with recruitment taking place in December and then April or May of the following year.

Since M. senhousia does not have annual rings, the

size-frequency method (Harding, 1949; Lewis and Taylor, 1967) was used to determine age structure of the population. Using the foregoing method, size compositions of age groups with standard errors were calculated (Table 5). Age compositions are summarized in Table 6. The Kolmogorov-Smirnov goodness-of-fit test only showed one significant deviation in the inflexion method (Table 3).

In order to substantiate the above results from the size-frequency method, commencing June 1975, over 100 representative bivalves were marked and placed adjacent to area III. The Bertalanffy (1930) growth equation was fitted to describe growth,

$$L_t = L (1 - e^{-k(t-t_0)})$$

where t is time, L_t is length at time t , L is asymptotic length, t_0 is the theoretical time when the animal is zero length and K is a constant that describes the growth rate to maximum size. Regression analysis and the Ford-Walford plot were used to determine the equation constants (Ralph and Maxwell, 1977; Sokal and Rohlf, 1969; Ebert, 1975). However, the recapture percent was low (Table 4). Approximately 9% ($N=101$) were recovered. Maximum growth is reached in roughly 11 years (Figure 7).

During nonrecruiting periods abundance was dominated by the two youngest age groups; the smallest exhibiting only a slight growth recession during late spring (Figure

8, Table 5). All older year classes have a greater deviation then, with a more pronounced fluctuation in the fall (September/October). Winter growth recessions were roughly in January (Figure 9). The densest recruitment (May, 1976) increased the total abundance by 93% (Table 6). Roughly 97.3% of this settlement was lost in one year. The 1⁺ and 2⁺ groups lost 82% and 30%, respectively, during the same period.

The biomass changes of standard sizes were monitored from October, 1975, through September, 1976 (Figure 9, Table 7). Pronounced fluctuations were noted in the larger sizes. Biomass reduction occurred in January, along with two other trends from April through June and also in August, both of which coincided with spawning periods.

Protothaca staminea

One thousand eight hundred and ninety specimens were examined (Figures 10 and 11). Since this bivalve has accentuated growth lines on the shell surface, the annular ring method was employed (Feder and Paul, 1973). Both size-frequency and biomass fluctuations were also monitored as in the mussel.

No apparent size-class movement took place within the transect (Figure 12). April and October, 1975, represent typical months, while July and February are months of recruitment and less growth, respectively.

Figure 13 shows the greatest abundance exists in areas II, III and IV, the other areas being primarily inhabited by small size groups. Recruitment occurs in May and July, the latter being more dominant.

Release and recovery, along with annular-ring methods were used. The recovery was low; roughly 13% (N=115) were found in area III, where they were initially released. Asymptotic growth is reached in about 15 years, according to the Bertalanffy equation (Figure 14, Table 8). Spawning occurs around May. The oldest groups reflect this fact by exhibiting less growth during this period, whereas the two youngest ages have only a winter recession (Figure 15, Table 9). The youngest year class dominated the population abundance when recruitment was high (Table 10). During the densest recruitment a 73% increase in abundance was noted with only 12% surviving one year later. The 1⁺ and 2⁺ age groups lost 50% and 75%, respectively, during this time.

The biomass changes of standard sizes were noted from October, 1975, through September, 1976 (Figure 16, Table 11). Major variations were seen in the larger sizes, such as those occurring during spawning and winter. The smaller size was not affected in the spawning period.

SUBSTRATE

Sediment analysis (Table 1) showed that the least populated areas, I and IV, exhibited average substrate

sizes of very coarse gravel and fine sand, respectively, whereas, the densest areas, II, III and IV, ranged from coarse to medium sand. The average corresponding tidal heights of these most abundant areas ranged from 1.10 m to .14 m (Table 2).

DISCUSSION

It can be seen by both the observed and calculated size increases that the Bertalanffy equation approximates the growth of both species. Fabens (1965) suggested that the fitted K values can be used for the interspecific comparisons as an index of intrinsic developmental rate. However, Ralph and Maxwell (1977) caution about erroneous K values if only a few of the age groups are represented. Even though only the younger age groups are represented in the venerid population, It can be seen that the monthly growth results indicate the same trends as exhibited by their respective K values. Musculus senhousia grows faster than Protothaca staminea, overall.

Growth rates of P. staminea appear to vary in different areas. Schmidt and Warne (1970) found similar growth rates to the Tomales Bay population in Mugu Lagoon, California. Paul and Feder (1973) found populations of P. staminea with very low growth rates in Galena Bay, Alaska. Lengths of approximately 20 mm were reached in seven years. Over the same span of time lengths of 50-60 mm were achieved in British Colombia (Quayle and Bourne, 1972), Long Beach, California (Knaggs, Pers. com.) and southern Alaska (Paul et al., 1976). In both Tomales Bay and Mugu Lagoon an approximate length of 38 mm was reached in a seven year period. The low growth rate of P. staminea in Alaska could be due to low temperatures. The general temperature

range was roughly 2-18 °C. Gilbert (1973) found similar geographical variations in growth rate in Macoma baltica and Dehnel (1956) in Mytilus californianus .

Distinct recruitment occurred in M. senhousia; no such tendency was exhibited by P. staminea. Two spawning periods, July and October, occur in the mussel population. Biomass fluctuations, regular gonadal inspection, and recruitment indicate that major spawning occurs around October. This spawning period took place during declining temperatures. Even though two recruitment periods were exhibited by P. staminea, regular gonadal inspection and biomass fluctuations indicate only one spawning. This is not incongruous, since different spawning periods could easily occur between exposed (coastal) and sheltered (bay) populations (Knaggs, pers. com.). The spawning period in Tomales Bay coincided with that found by Quayle and Borne in British Colombia (1972), but conflicts with that of Fraser and Smith (1928) who reported spawning occurring in February/March. It also approximates with that estimated in Monterey, California (Haseltine, pers. com.). The venerid tends to spawn around April and May when the temperature is increasing after a preceding decrease.

In conjunction with larger recruitment, M. senhousia also experiences greater mortality than P. staminea. Seed (1969) felt fast-growing bivalves could 'outgrow' the limits imposed by their environment, resulting in comparatively

early mortality.

Smaller Musculus senhousia tended to live higher intertidally than the larger ones. This adds support to Seed's (1969) statement of larger bivalves tending to exist more abundantly lower intertidally due to greater food availability and less chance of physical stress, such as dessication, even though predators exist more abundantly in the lower area, also. Even though the same tendency was found by Schmidt and Warne (1970) for P. staminea in southern California, it did not occur in Tomales Bay. Additionally, it was found in Galena Bay, Alaska, that the intertidal distribution of P. staminea was influenced by tidal height (Paul et al., 1973). The smaller clams tended to exist lower intertidally while the larger groups (20 mm) exhibited a converse trend. Gilbert (1973) noted a similar situation in which Macoma baltica at .34 m above MLW grew faster than those below this height. This was primarily due to decreased temperature in the lower intertidal.

M. senhousia has only been reported on mud flats and pilings (Hanna, 1954). P. staminea, however, has been reported on beaches of coarse sand or fine gravel (Fraser and Smith, 1928). In this study, P. staminea occurred most abundantly in coarse to medium sand. However, the upper and lower extremes consisted of very coarse gravel and fine sand, respectively, agreeing with Fraser's belief that P. staminea does not exist well in fine sand.

SUMMARY

1. Musculus senhousia reaches asymptotic size at an earlier age than Protothaca staminea.
2. The survival rate of M. senhousia is greater than that of P. staminea in older age groups.
3. Larger recruitment occurs with M. senhousia than with P. staminea.
4. P. staminea spawns only once in the spring, while M. senhousia exhibits two spawnings, spring and fall.
5. Greater mortality occurs amongst the younger age groups in the population of M. senhousia than in that of P. staminea.
6. Smaller sizes of M. senhousia tend to predominate in the upper intertidal areas, while the larger sizes are lower. No such effect occurs in the P. staminea population.
7. The overall substrate preference for both populations ranges from coarse to medium sand.
8. Maximum population abundance occurred between the tidal heights 1.10 m to .28 m of both species.

AUTHOR'S NOTE ON ANNUAL GROWTH

Studies of age structure provide estimates of population characteristics such as average growth rate and maximum longevity (Schmidt and Warne, 1970). Generally, three methods have evolved for examining growth: (1) size frequency; (2) release and recovery; (3) interpretation of slow-growth periods on the shells (Haskin, 1954). Thus an age, in years, and a record of growth rate for each shell can be determined (Feder and Paul, 1973; Quayle and Bourne, 1972; Schmidt and Warne, 1970). However, age determinations based solely upon one of the above methods are doubtful, and the study should be supplemented by additional information from one of the remaining techniques (Berta, 1976; Haskin, 1954; Negus, 1966; Seed, 1969). Even experienced investigators have erroneously aged specimens (Knaggs, pers. com.). Not only has it been found that the same species in adjacent populations can exhibit great variations in growth, but also specimens both with and without annual rings have been observed in the same species (Fraser and Smith, 1928; Gilbert, 1973). Additionally, it has been shown that each time bivalves are removed from their habitat, growth stops and a disturbance ring is formed (Quayle, 1951). While Harding's (1949) inflexion method is a convenient statistical technique for separating size groups in populations, the foregoing problems in determining age should be kept in mind when ages are assigned to specific size groups.

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Fish and Game. Address: 2201 Garden Rd., Monterey, CA.

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Shore, Long Beach, CA.

Table 1. Average median grain sizes from April, 1975, through September, 1976.

Area	Number of samples	phi units	Sediment description
I	17	-.788	very coarse gravel
II	16	.273	coarse sand
III	17	.813	coarse sand
IV	17	1.321	medium sand
V	18	2.251	fine sand

Note: All areas exhibited poor sorting

Table 2. Tidal heights ($\bar{X} \pm \text{S.E.}$) of upper limit of each area, from April 1975, through September, 1976.

Area	Number of samples	Tidal height in meters
I	18	$1.45 \pm .02$
II	18	$1.10 \pm .01$
III	18	$.66 \pm .01$
IV	18	$.28 \pm .01$
V	18	$.14 \pm .01$

Table 3. Kolmogorov-Smirnov results in testing for goodness of fit of inflexion method.

Date	D. _{.05}	D. _{.01}	D. _{.001}	D _{max.}	Number of comparisons
A 1975	.03385	-	-	.01927 ¹	42
M	.04519	-	-	.02658 ¹	38
J	.05596	-	-	.03396 ¹	40
J	.06939	-	-	.01828 ¹	43
A	.06807	-	-	.02764 ¹	45
S	.06445	-	-	.02027 ¹	42
O	.07089	-	-	.03162 ¹	47
N	.07442	-	-	.02402 ¹	45
D	.06731	-	-	.01966 ¹	44
J 1976	.09198	-	-	.03211 ¹	47
F	.10572	-	-	.03030 ¹	43
M	.02837	.03401	.03991	.04188 ²	39
A	.03927	-	-	.03094 ¹	41
M	.06756	-	-	.01733 ¹	45
J	.08158	-	-	.02166 ¹	49
J	.08219	-	-	.02564 ¹	42
A	.07751	-	-	.01954 ¹	43
S	.08935	-	-	.04329 ¹	43
					<u>778</u> Total

1- not significant

2- $P > .001$

Table 4. Musculus senhousia growth data.
Sample no. = 9

Growth ring no.	Sample no.	Mean measured length (mm)	Length calculated from Bertalanffy equation (mm)
1	2	10.01	9.12
2	1	14.03	14.03
3	0	18.03 ¹	18.60
4	3	20.79	20.94
5	1	22.93	22.42
6	0	23.88 ¹	23.36
7	0	-	23.96
8	1	24.12	24.34
9	0	-	24.58
10	1	24.75	24.73
11	0	-	24.83
12	0	-	24.89

Bertalanffy equation constants: $L = 25.00$, $K = .4543$

1- data derived from table

Table 5. Size (shell length $\bar{X} \pm$ S.E. in mm) composition of M. senhousia on each sampling date.

Date	Age Class						
	0 ₂ ⁺	0 ₁ ⁺	1+	2+	3+	4+	5+
1975							
A		3.41 [±] .33	6.22 [±] .64	9.43 [±] 1.22	14.31 [±] 1.51	19.11 [±] 1.53	20.63 [±] 2.62
M		5.03 [±] .54	7.63 [±] .51	10.61 [±] .51	15.74 [±] 1.45	19.82 [±] .63	
J		5.86 [±] 7.11	8.49 [±] .62	11.74 [±] 1.29	16.63 [±] 1.47	19.73 [±] 1.24	22.53 [±] 3.19
J		5.83 [±] 2.71	10.87 [±] 1.28	15.11 [±] 1.14	18.33 [±] 1.50	20.91 [±] .93	22.94 [±] 3.41
A		6.34 [±] 2.33	11.13 [±] 1.32	15.31 [±] 1.19	18.37 [±] 2.41	19.94 [±] 1.63	22.21 [±] 2.69
S		8.41 [±] 1.93	11.90 [±] 1.76	17.56 [±] 1.14	19.82 [±] 1.23	21.95 [±] 1.31	23.88 [±] 4.09
O		7.68 [±] 3.73	13.11 [±] 1.43	18.19 [±] 1.39	20.68 [±] .63	22.48 [±] 1.62	
N		8.62 [±] 2.29	13.06 [±] 1.68	18.58 [±] 2.79	21.63 [±] .88	23.19 [±] 1.08	24.66 [±] 1.58
D	2.61 [±] 1.08	8.59 [±] 1.88	13.39 [±] 1.28	18.76 [±] 1.48	21.83 [±] 1.87	23.86 [±] 2.18	
1976							
J	3.66 [±] 2.48	9.09 [±] 1.87	13.04 [±] 1.99	18.68 [±] 2.29	21.69 [±] 3.88	24.06 [±] 3.86	
F	5.59 [±] 2.76	10.38 [±] 1.96	14.47 [±] 2.00	19.06 [±] 3.47	22.31 [±] 4.21		24.93 [±] 3.96
M	3.41 [±] 1.99	10.49 [±] 2.87	15.68 [±] 2.66	18.89 [±] 3.08			
A	5.08 [±] 3.88	11.36 [±] 1.53	15.19 [±] 1.79	19.19 [±] 2.53	21.58 [±] 1.83		
M	6.69 [±] 1.76	13.31 [±] 1.23	15.88 [±] 1.53	19.04 [±] 1.36	21.53 [±] 3.08		
J	6.79 [±] 2.69	13.11 [±] 1.53	15.94 [±] 1.11	19.19 [±] 2.19	21.83 [±] 1.57		25.13 [±] 4.81
J	8.58 [±] 2.11	13.43 [±] 1.50	16.48 [±] 1.34	19.20 [±] 1.29	21.59 [±] 1.99		
A	10.31 [±] 2.19	15.16 [±] 1.48	18.46 [±] 4.88	20.10 [±] 1.09	22.53 [±] 2.01		
S	11.36 [±] 1.75	15.48 [±] 1.96	18.50 [±] 1.68	20.29 [±] 2.26	23.00 [±] 1.87		

0_1^+ and 0_2^+ represent 1975 and 1976 recruitment, respectively.

Table 6. Age composition ($\# \text{ m}^{-2}$) of M. senhousia on respective sampling dates

Date	Age Class							
	0_2^+	0_1^+	1^+	2^+	3^+	4^+	5^+	Total
1975								
A	0	3,164	1,282	390	353	133	33	5,357
M	0	812	1,182	556	229	226	0	3,005
J	0	432	908	536	316	132	32	2,356
J	0	140	850	365	390	130	40	1,915
A	0	275	760	335	215	165	40	1,790
S	0	275	1,010	400	330	150	50	2,215
O	0	280	935	375	155	85	0	1,830
N	0	375	875	225	95	70	25	1,665
D	145	335	1,175	245	105	30	0	2,035
1976								
J	80	305	570	56	32	32	0	1,075
F	65	305	340	70	25	0	25	830
M	8,604	320	240	52	0	0	0	9,180
A	4,180	348	212	36	8	0	0	4,784
M	880	340	292	76	24	0	0	1,612
J	448	223	280	72	52	0	32	1,107
J	352	336	276	96	24	0	0	1,084
A	380	372	200	76	24	0	0	1,052
S	232	188	164	112	56	0	0	752

0_1^+ and 0_2^+ represent 1975 and 1976 recruitment, respectively.

Table 7. Seasonal variations ($\bar{X} \pm \text{S.E.}$) in dry flesh weight (mg.) of M. senhousia of standard sizes (6mm, 12mm, 18mm).

Date	Standard Sizes		
	6mm	12mm	18mm
(1975)O	2.61 \pm .91	13.03 \pm 1.49	21.53 \pm 2.41
(1976)J	1.59 \pm .78	8.31 \pm .91	19.53 \pm 5.31
M	3.40 \pm 1.10	18.92 \pm 1.35	43.06 \pm 1.72
A	3.55 \pm 1.15	16.45 \pm 1.75	44.69 \pm 4.08
M	2.50 \pm .50	15.09 \pm 1.62	39.39 \pm 1.30
J	4.25 \pm 3.15	11.23 \pm 1.49	33.12 \pm 4.63
J	1.65 \pm .25	9.03 \pm .69	33.15 \pm 1.63
A	2.51 \pm 1.71	13.30 \pm .80	40.96 \pm 7.68
S	1.85 \pm .35	12.15 \pm 2.15	25.75 \pm .73

Table 8. Protothaca staminea growth data.

Sample no. = 15

Growth ring no.	Sample no.	Mean measured height (mm)	Height calculated from Bertalanffy equation (mm)
1	9	11.59	10.52
2	4	14.91	18.03
3	0	22.68 ¹	23.39
4	1	26.89	27.23
5	0	-	29.96
6	0	-	31.91
7	1	32.33	33.31
8	0	-	34.31
9	0	-	35.02
10	0	-	35.53
11	0	-	35.89
12	0	-	36.15
13	0	-	36.34
14	0	-	36.47
15	0	-	36.56
16	0	-	36.63

Bertalanffy equation constants: $H = 36.8$, $K = .3365$

1- data derived from table

Table 9. Size (shell height $\bar{X} \pm$ S.E. in mm) composition of P. staminea at each sampling

Date	Age Class						
	0 ₄ ⁺	0 ₃ ⁺	0 ₂ ⁺	0 ₁ ⁺	1 ⁺	2 ⁺	3 ⁺
1975							
A				6.13 [±] .14	10.07 [±] 1.3		
M				6.41 [±] .22		14.36 [±] .63	22.71 [±] 1.35
J				6.96 [±] .31	11.40 ²	14.10 [±] .81	
J			5.43 [±] .277	9.14 [±] .27	12.25 [±] .30	13.73 [±] .71	25.29 [±] 1.02
A ¹			8.69 [±] .39		12.48 [±] 1.89	15.62 [±] .79	
S			8.97 [±] .24		13.05 [±] 1.09	17.49 [±] .89	
O			9.02 [±] .56		13.40 ²	17.83 ²	
N			9.26 [±] .39		13.83 [±] 1.42	18.30 [±] 1.45	26.26 [±] 1.94
D			9.85 [±] .42		13.38 [±] .34	17.82 [±] 1.83	
1976							
J			9.47 [±] .36		12.36 [±] .20		
F			9.21 [±] .47		13.51 ²		
M		5.88 [±] .48	11.71 [±] 1.14			20.19 ²	
A		6.40 [±] .57	11.69 [±] .27		16.31 [±] 1.46	23.11 [±] .68	27.17 [±] 1.68
M		7.22 [±] .48	11.86 [±] .24		14.38 [±] .12		
J		8.57 [±] .63	12.25 [±] .66		14.56 [±] .67	22.21 ²	
J	4.83 [±] .25	9.20 [±] .32	13.37 [±] .46		17.49 [±] 1.28	22.60 [±] 1.00	
A ¹	8.13 [±] 1.10		13.61 [±] .74		18.09 [±] 1.73		
S	8.81 [±] .91		14.03 [±] .92		18.41 [±] 1.43	24.82 [±] 2.17	

1. Recruitment overlapped too greatly to be separated. 0_1^+ , 0_2^+ and 0_3^+ , 0_4^+ represent 1975 and 1976 settlement, respectively.

2. No replicates.

Table 10. Age composition (# m⁻²) of P. staminea on respective sampling dates

Date	Age Class							Total
	0 ₄ ⁺	0 ₃ ⁺	0 ₂ ⁺	0 ₁ ⁺	1 ⁺	2 ⁺	3 ⁺	
1975								
A				554	33			587
M				463		25	7	495
J				380	16	20		416
J			860	180	40	30	10	1,120
A ¹				685	70	20	5	780
S				465	65	20		550
O				383	52	23		468
N				260	40	15	25	340
D				310	50	10		370
1976								
J				246	41	4	6	297
F				230	35			265
M		428		125		15		568
A		280		65	15	10	10	380
M		316		108	32	5		469
J		292		84	20	5		401
J	757	104		68	40	12		981
A ¹		348		56	33			437
S		326		51	27	9		413

1. Recruitment overlapped too greatly to be separated.
 0₁⁺, 0₂⁺ and 0₃⁺, 0₄⁺ represent 1975 and 1976 settlement,
 respectively.

Table 11. Seasonal variations ($\bar{X} \pm S.E.$) in dry flesh weight (mg.) of P. staminea of standard sizes (7mm, 14mm, 21mm).

Date	Standard Sizes		
	7mm	14mm	21mm
(1975)O	4.03 \pm .95	36.41 \pm 4.31	84.32 \pm 6.59
(1976)J	2.02 \pm .73	27.21 \pm 3.41	70.63 \pm 9.31
M	5.85 \pm .05	35.33 \pm 2.02	104.91 ^a
A	5.03 \pm .69	31.73 \pm 1.34	84.45 \pm 5.35
M	4.90 \pm 1.40	25.62 \pm .93	56.51 \pm 4.31
J	2.67 \pm .64	26.33 \pm 3.18	58.15 \pm 1.45
J	3.60 \pm .10	20.87 \pm 2.51	69.03 \pm 3.21
A	3.46 \pm .98	31.70 \pm 7.30	71.45 \pm 6.65
S	3.00 \pm 1.00	33.30 \pm 6.50	73.95 \pm 5.25

a- only 1 sample

Figure 1. Sampling site in Tomales Bay

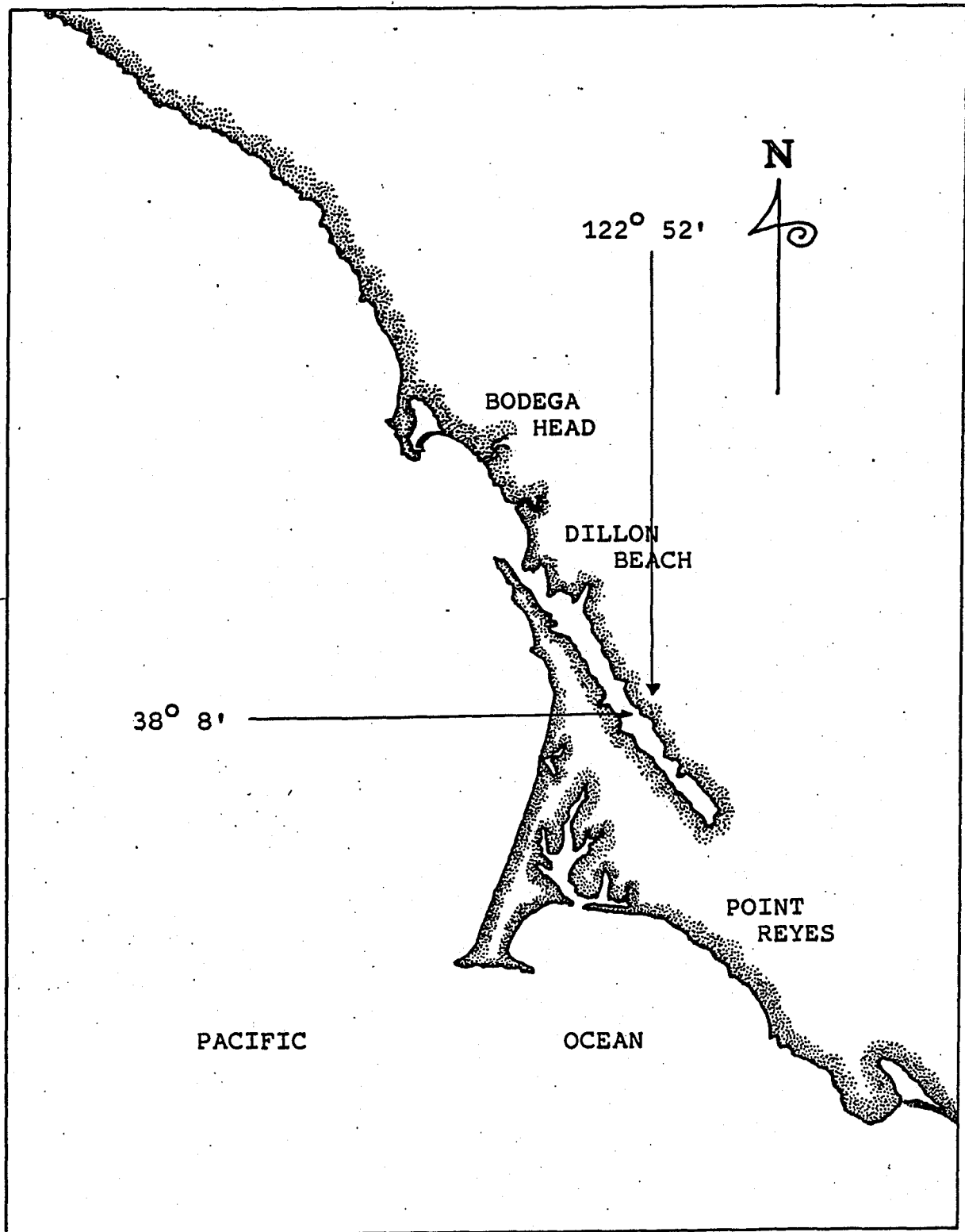


Figure 2. Temperature fluctuations in areas I and IV from April, 1975, through September, 1976. Lower line in each area represents the minimum temperature, while the upper line is the maximum.

Temperature °C

Area IV

Area I

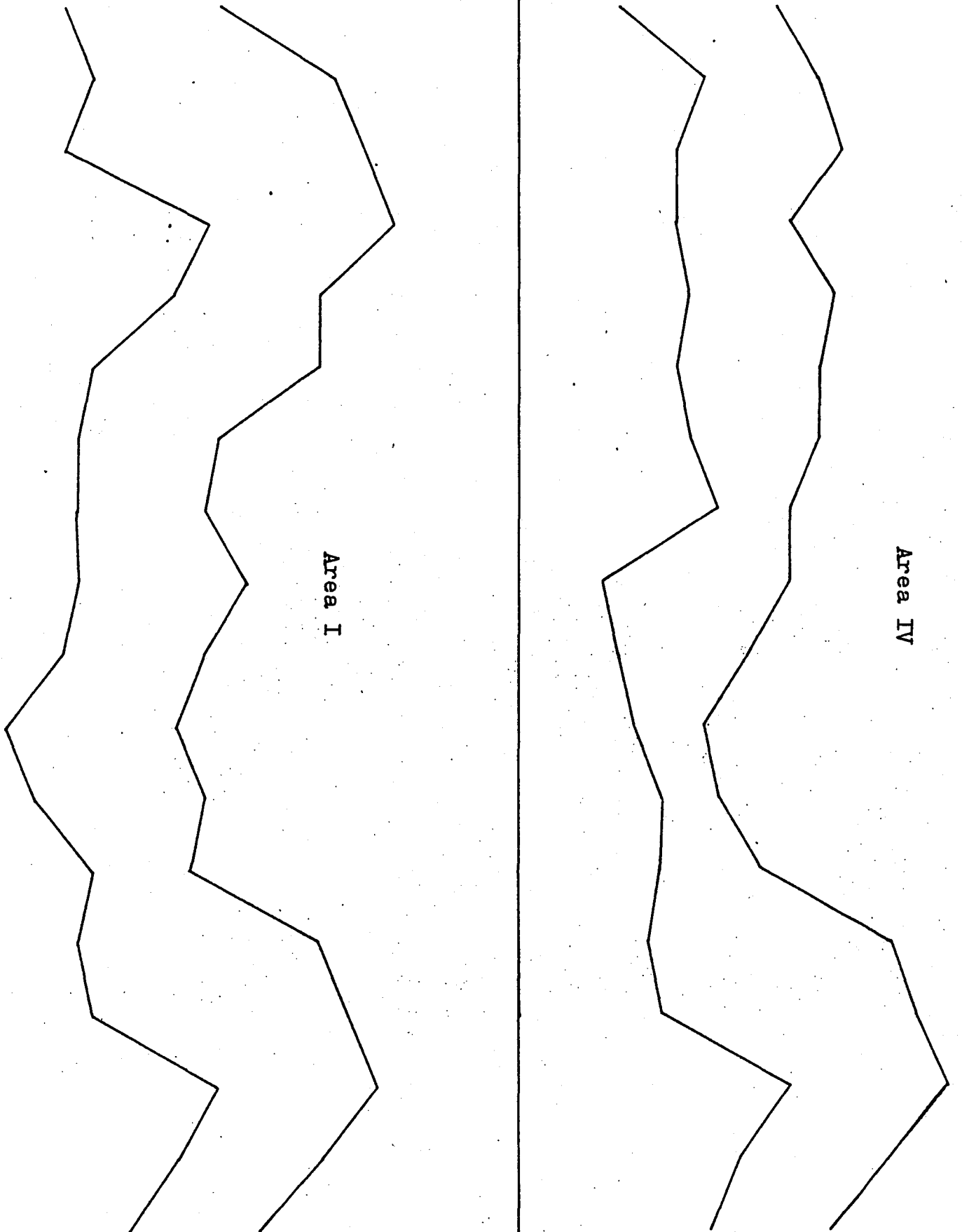


Figure 3. Total monthly abundance of Musculus senhousia from April, 1975, through September, 1976. Bars represent monthly means, vertical lines the 95% confidence intervals, and the dashed line the overall mean.

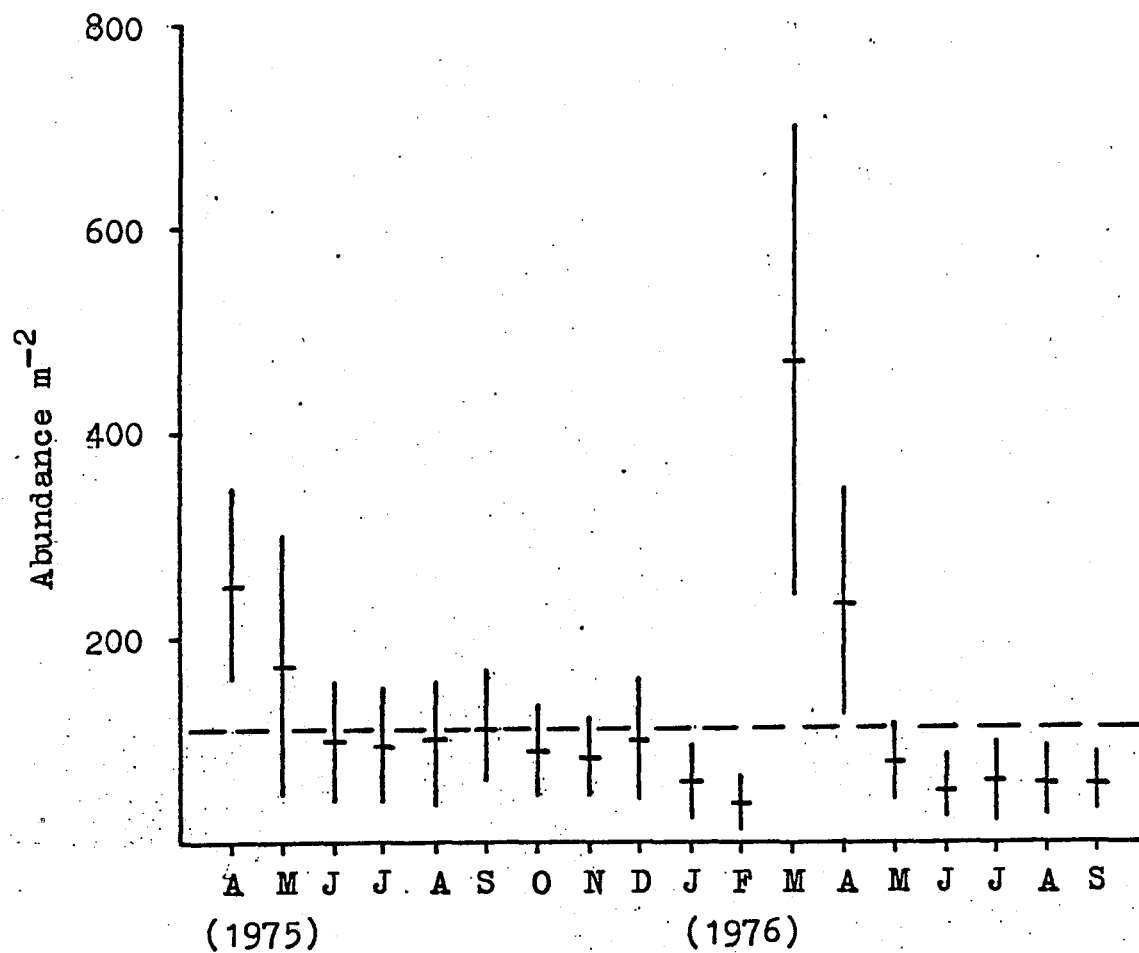


Figure 4. Size-frequency distributions of
M. senhousia from April, 1975, through September,
1976. N = total monthly abundance.

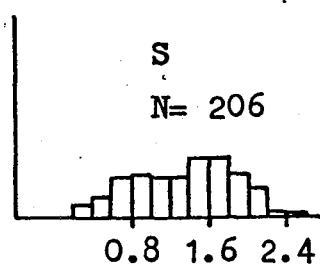


Figure 5. M. senhousia size-frequency distribution of each area, from high (I) to low (V) intertidal areas, in the transect at representative times. N = abundance of each area, respectively.

Frequency (percent)

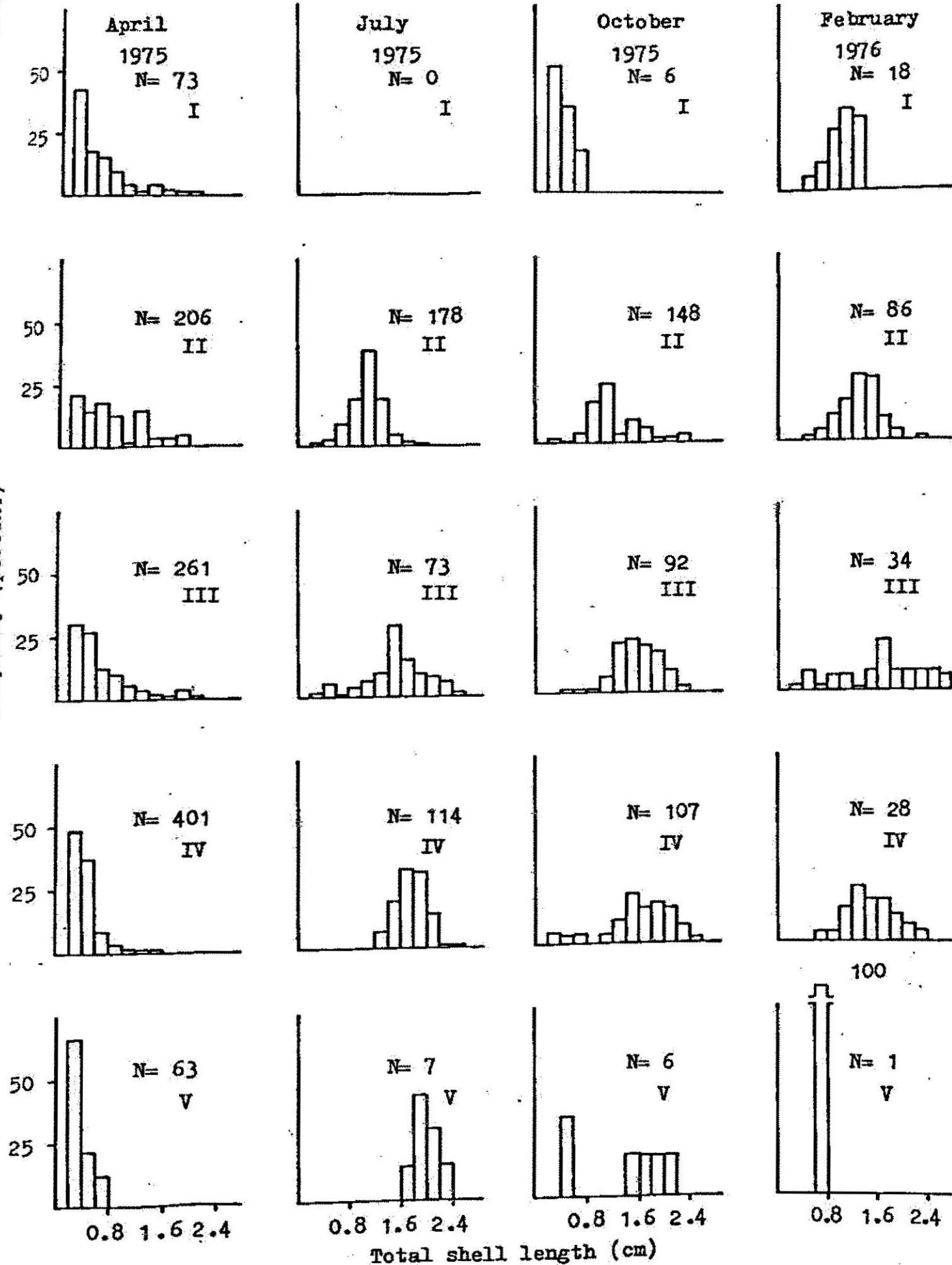
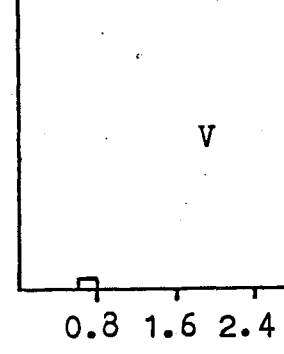
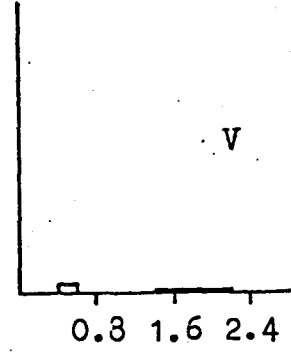
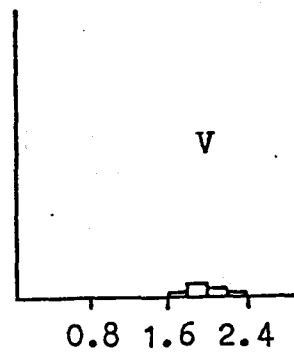
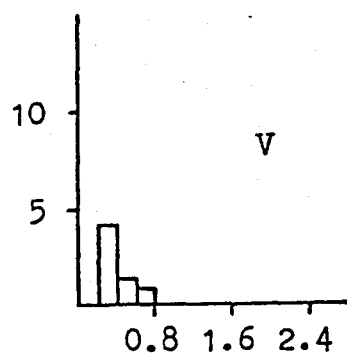
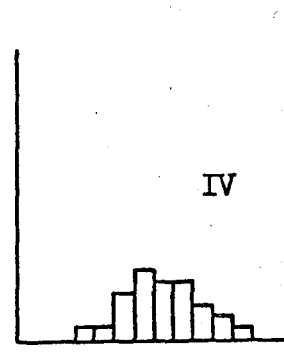
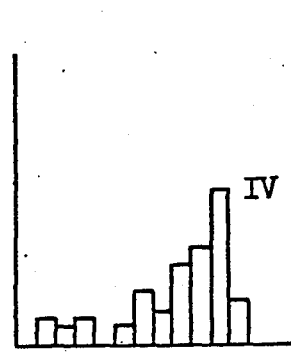
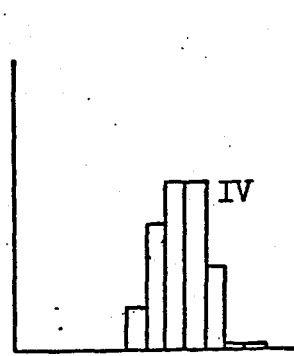
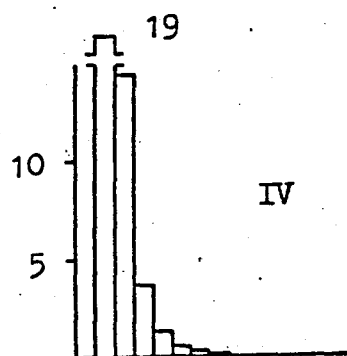
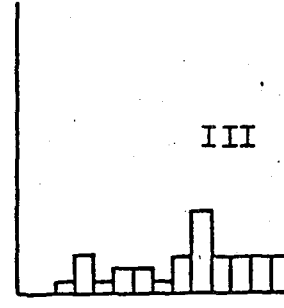
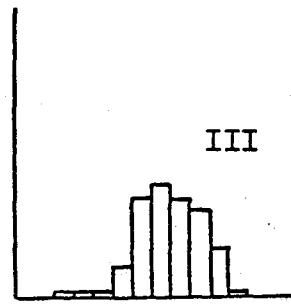
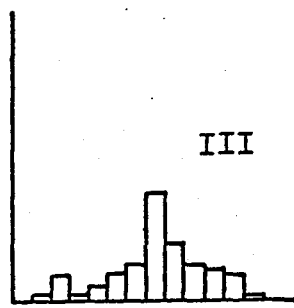
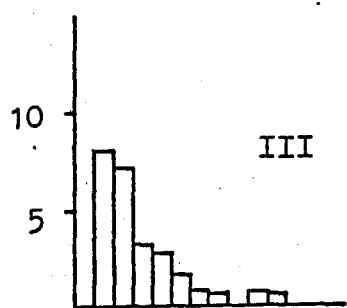
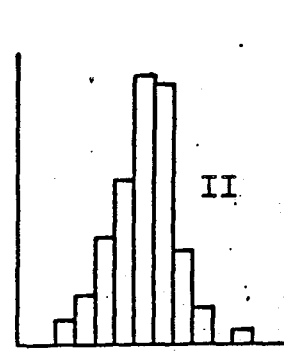
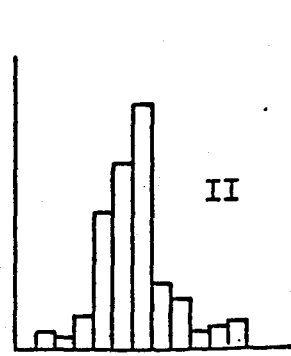
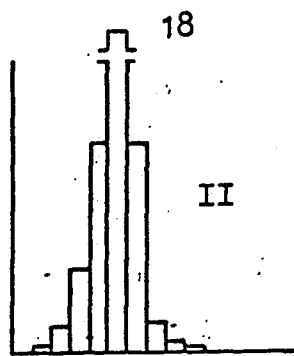
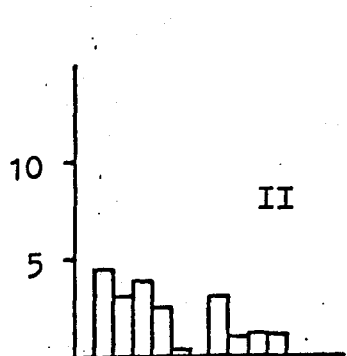
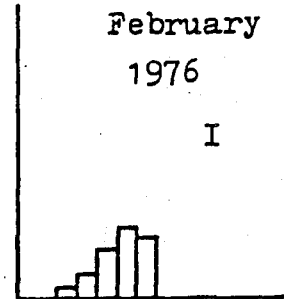
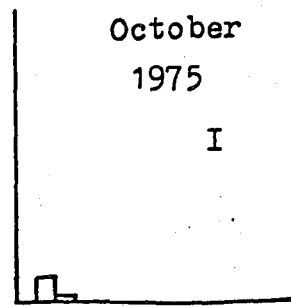
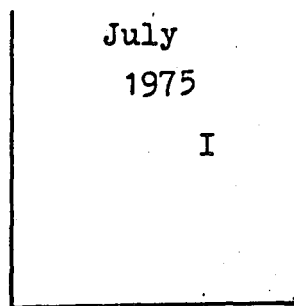
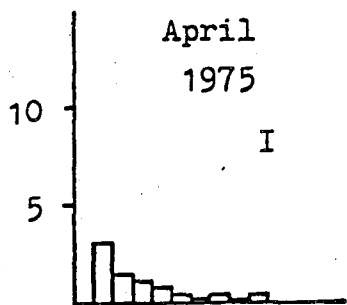


Figure 6. Size-frequency distribution of M. senhousia in the same areas as fig.3 , but total monthly abundance of entire transect was used.

Frequency (percent)



Total shell length (cm)

Figure 7. Ideal growth curve of M. senhousia derived
by von Bertalanffy growth equation.

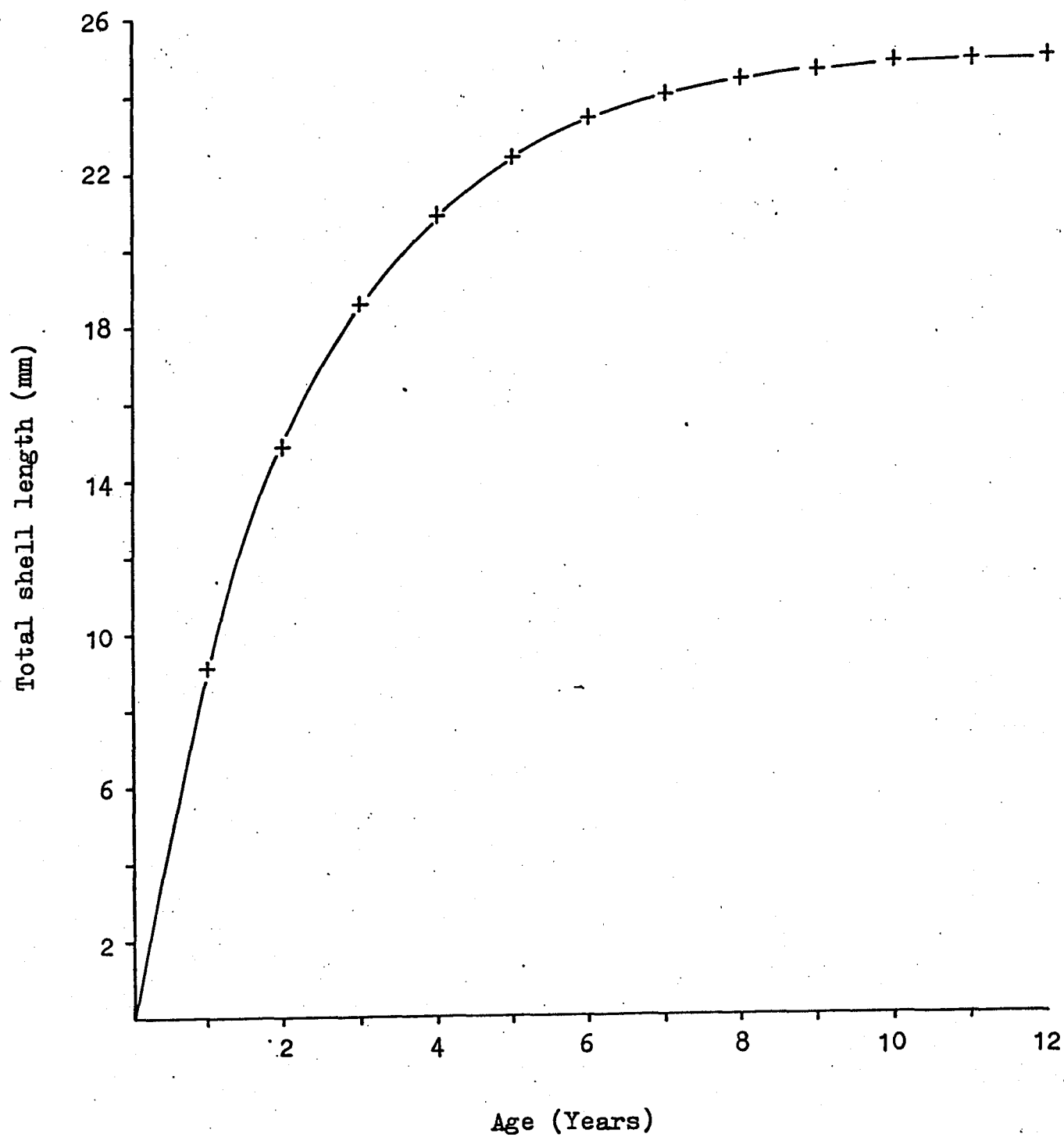


Figure 8. Mean shell length (cm) of each year class of M. senhousia on each sampling date. Recruitment of 1975 and 1976 is represented by 0_1^+ and 0_2^+ , respectively.

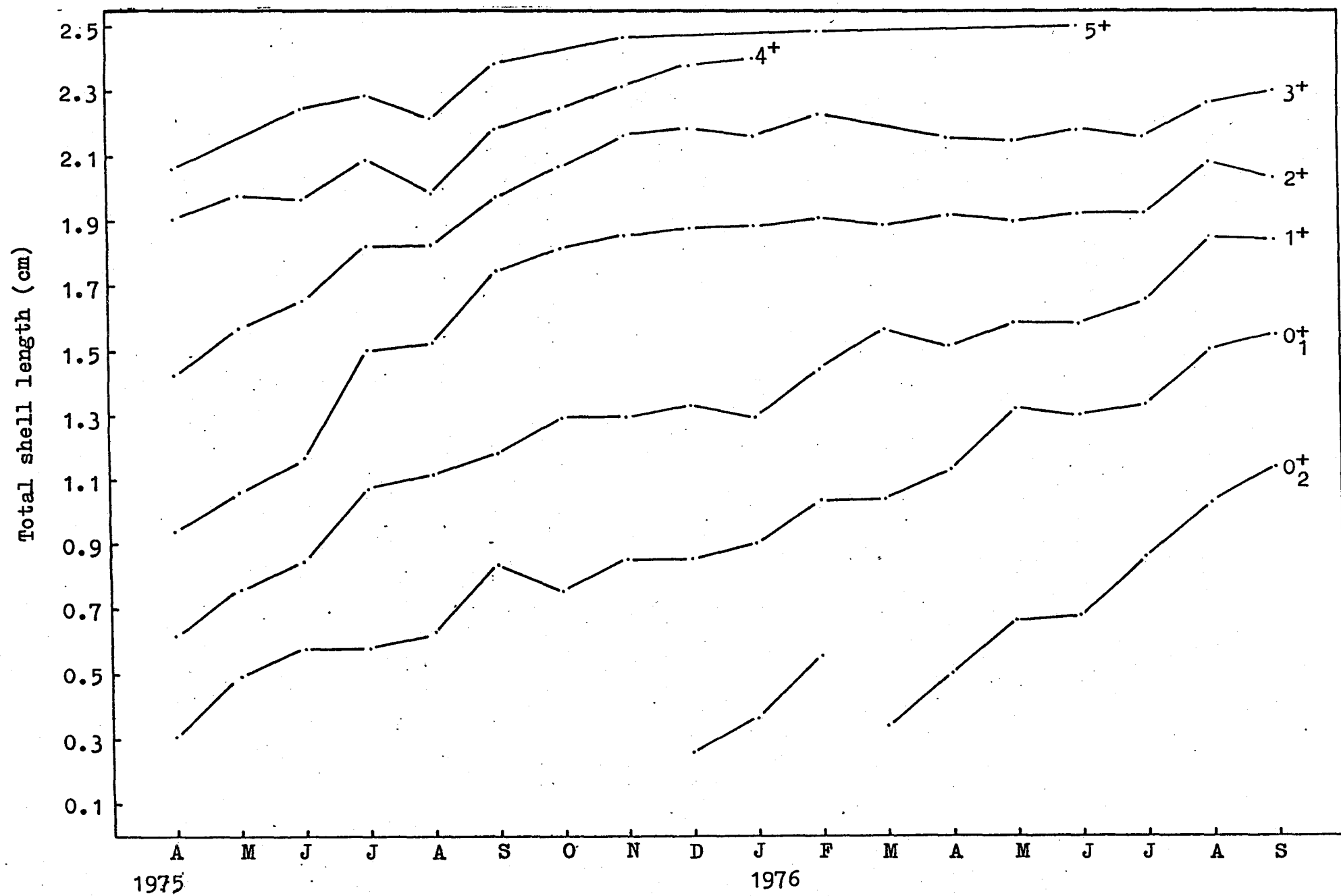


Figure 9. Seasonal variation in dry flesh weight
(mg.) of M. senhousia of standard sizes (6, 12, 18 mm).

Flesh Weight (mg. dry wt.)

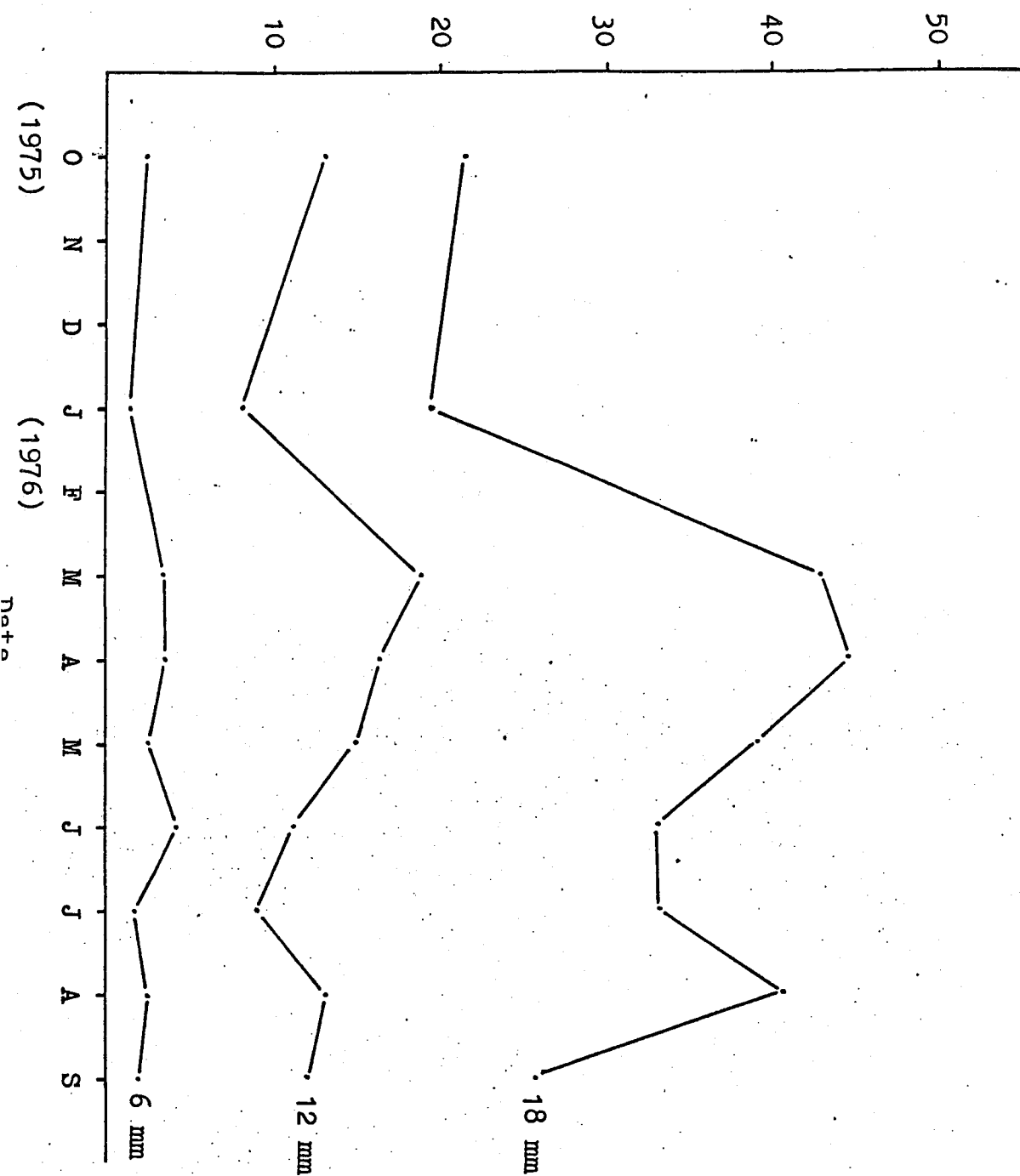


Figure 10. Total monthly abundance of Protothaca
staminea from April, 1975, through September, 1976.
Bars represent monthly means, vertical lines the 95%
confidence intervals, and the dashed line the overall
mean.

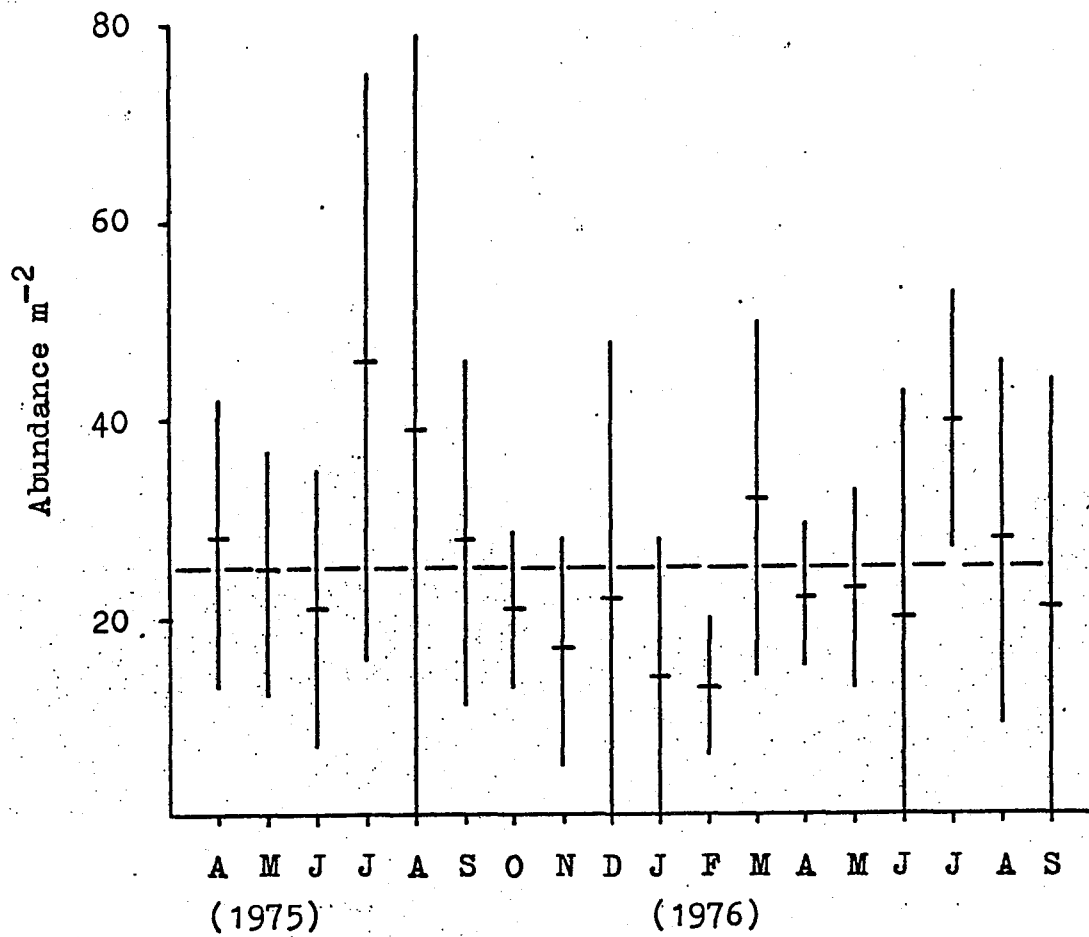


Figure 11. Size-frequency distributions of
P. staminea from April, 1975, through September,
1976. N = total monthly abundance.

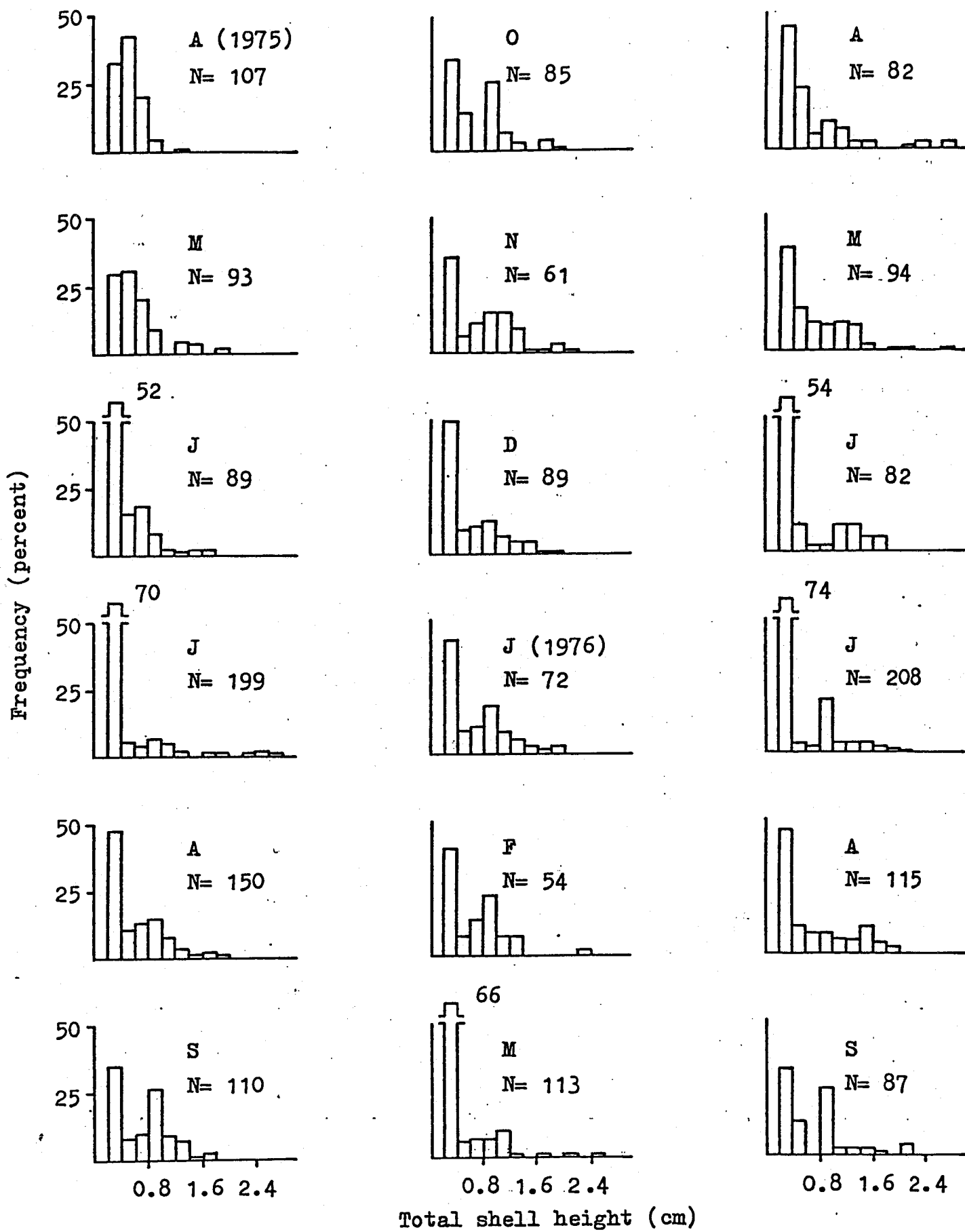


Figure 12. Size-frequency distribution of P. staminea of each area, from high (I) to low (V) tidal heights, over the transect at representative times. N = abundance of each area, respectively.

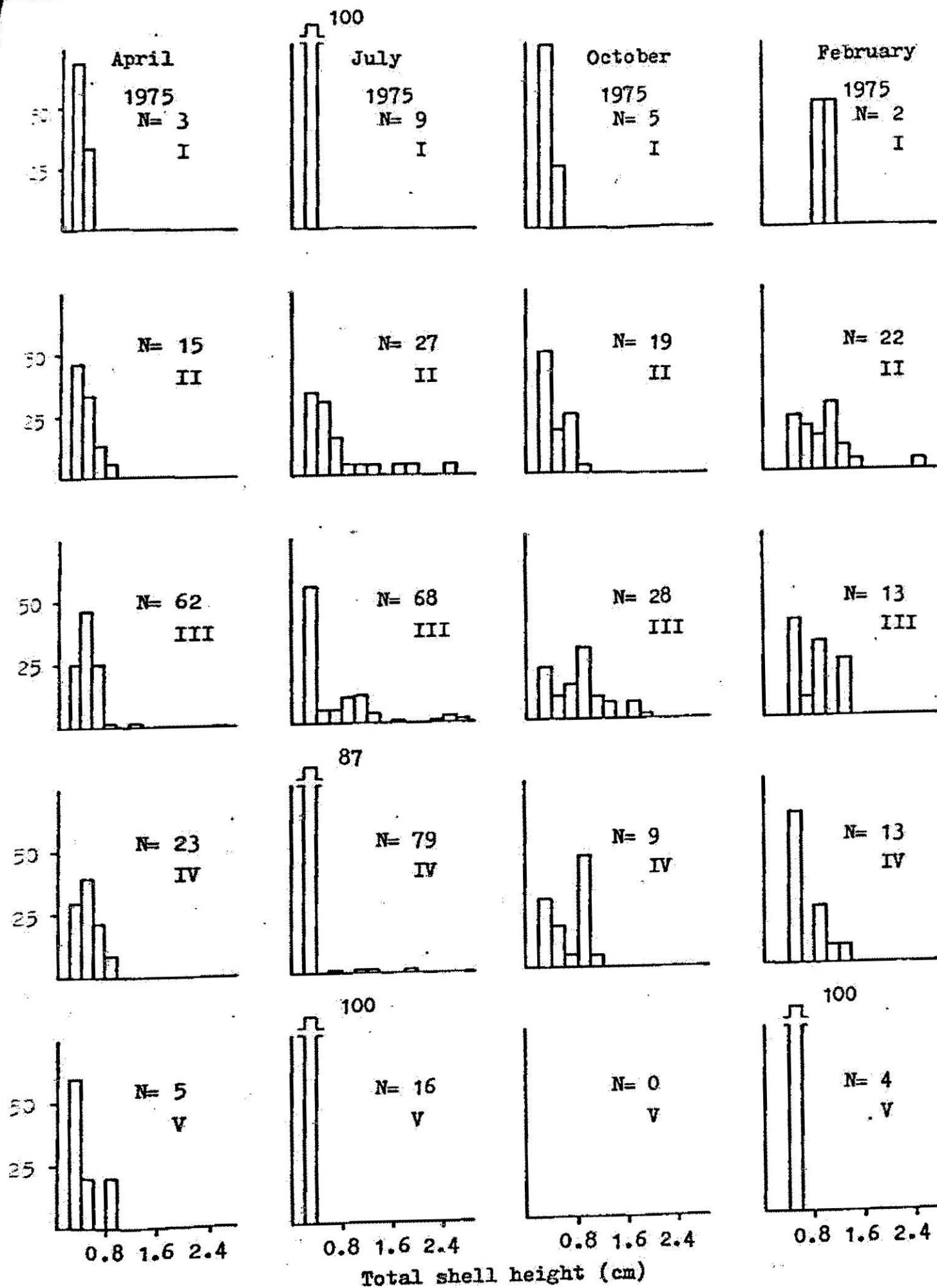


Figure 13. Size-frequency distribution of
P. staminea in same areas as fig.11, but total
monthly abundance of entire transect was used.

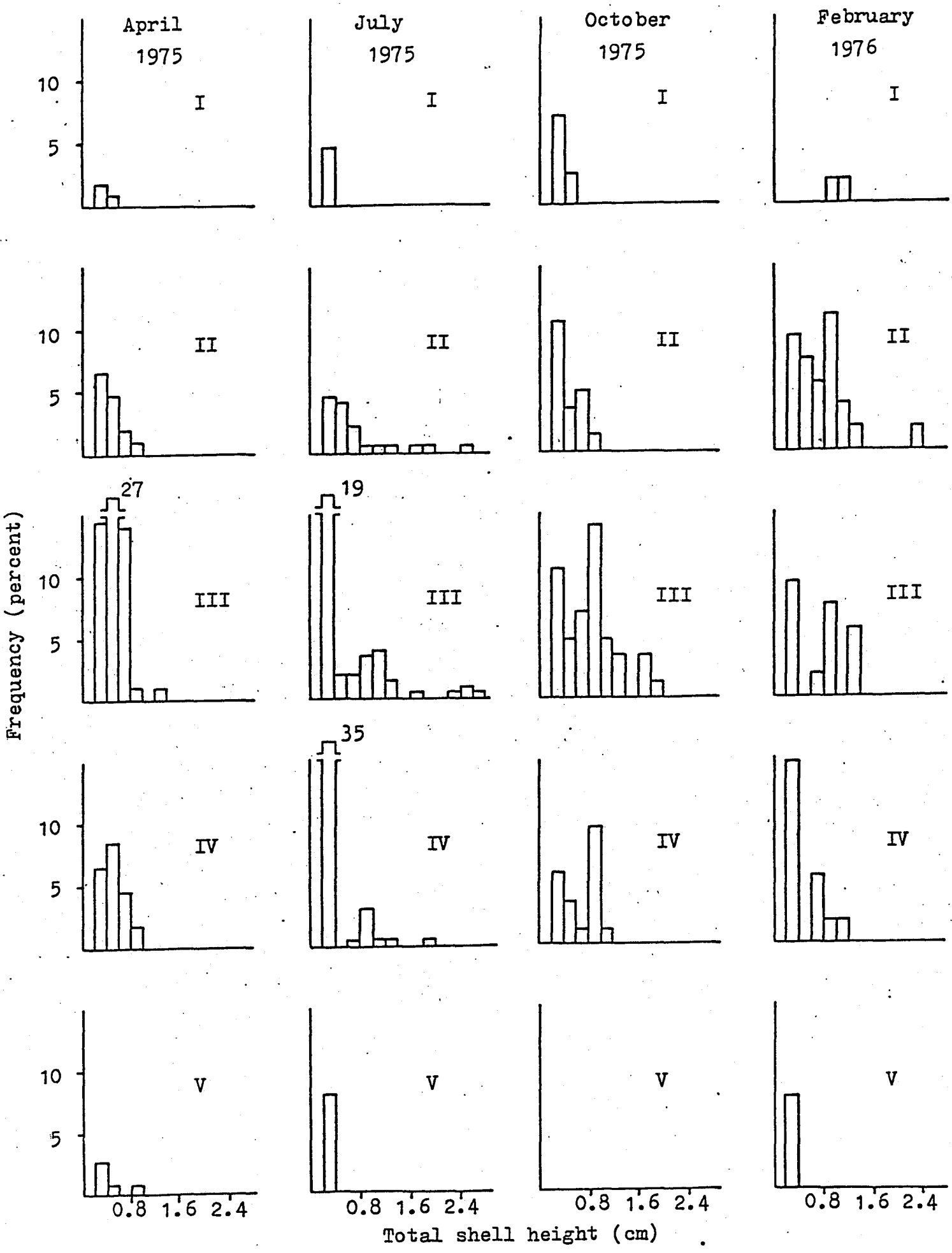


Figure 14. Ideal growth curve of P. staminea
derived by von Bertalanffy growth equation.

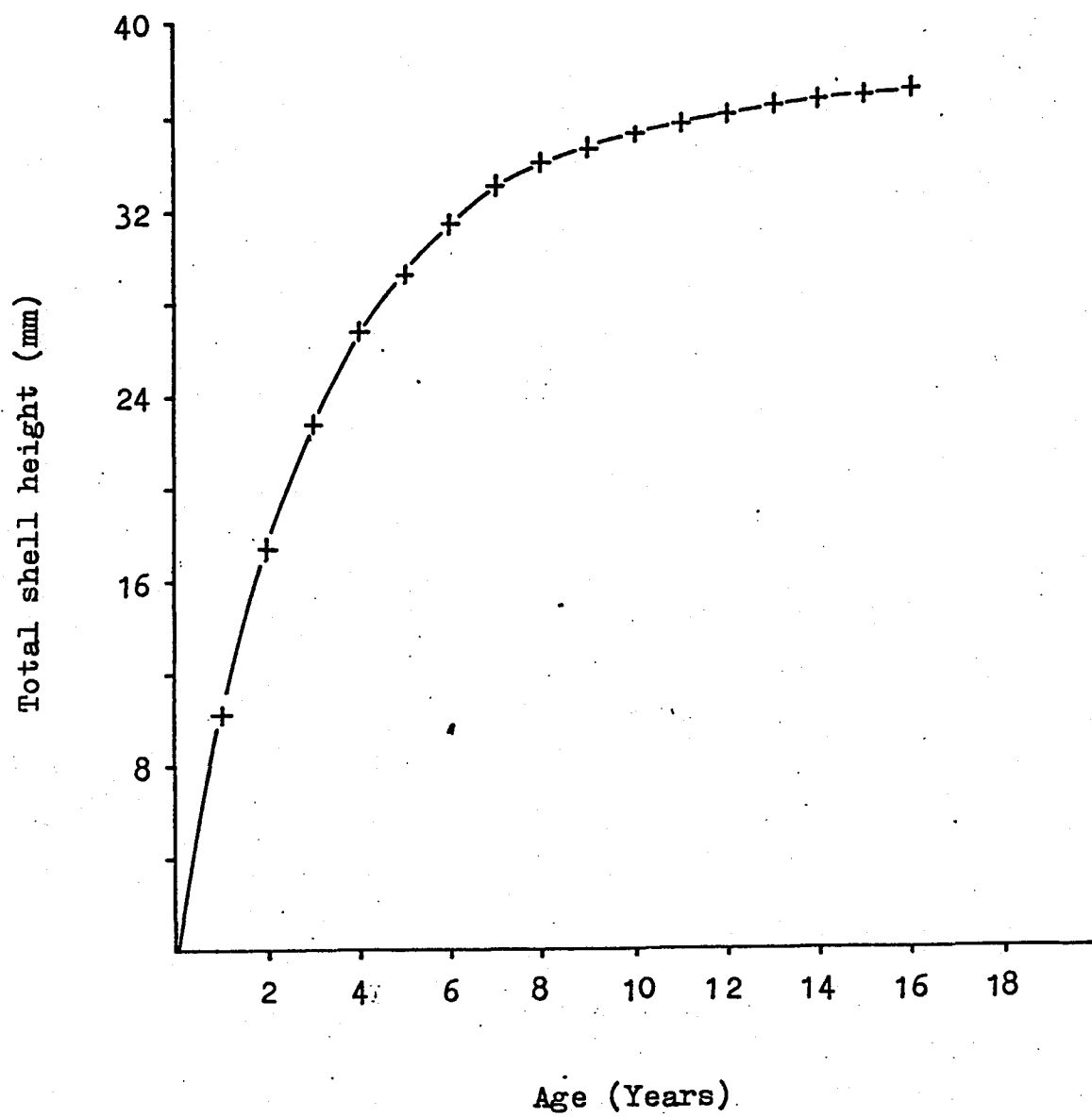


Figure 15. Mean shell height (cm.) of each year class of P. staminea on each sampling date. O_1^+, O_2^+ and O_3^+, O_4^+ represent 1975 and 1976 settlement, respectively.

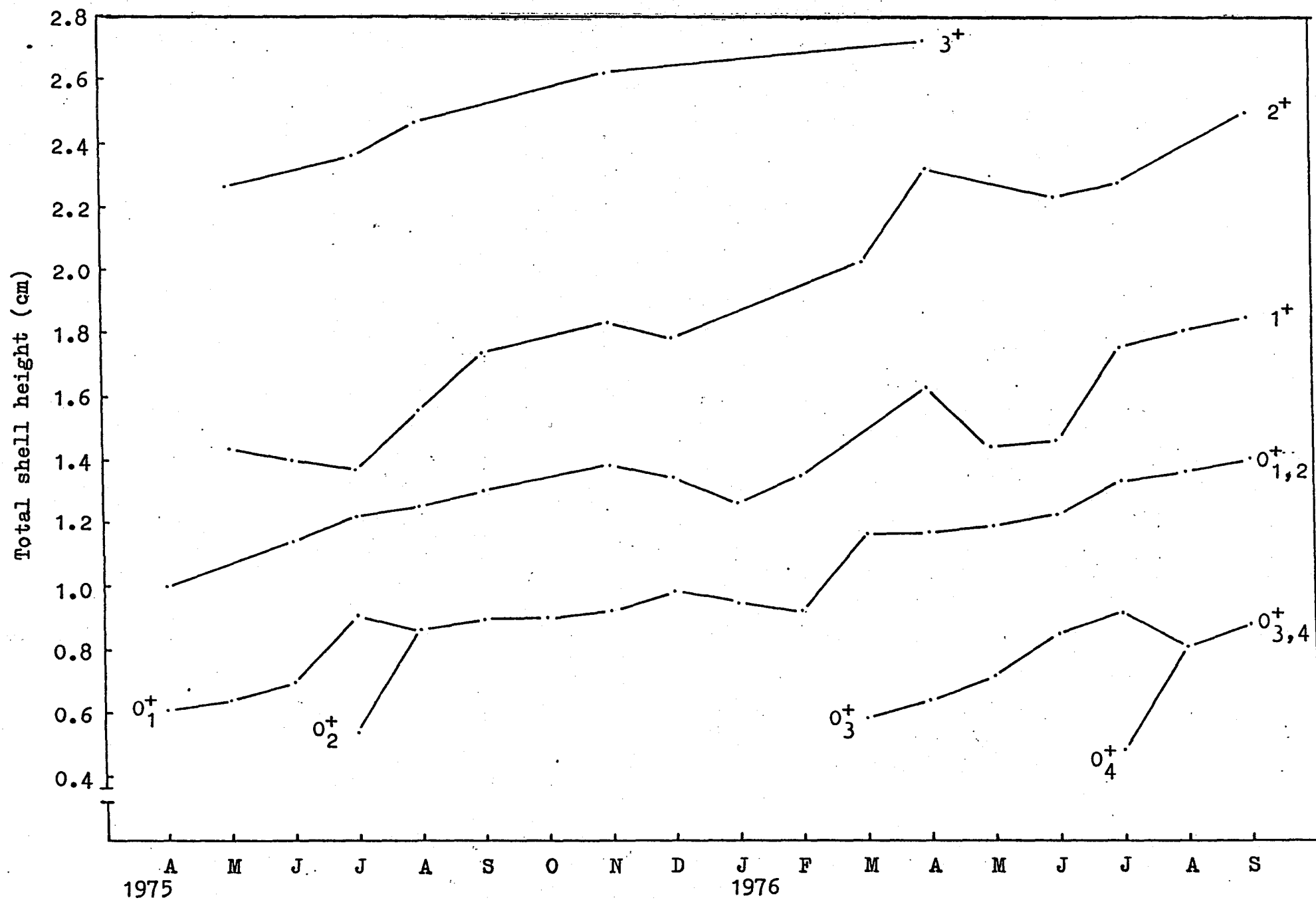


Figure 16.. Seasonal variation in dry flesh weight
(mg.) of P. staminea of standard sizes (7, 14, 21 mm.).

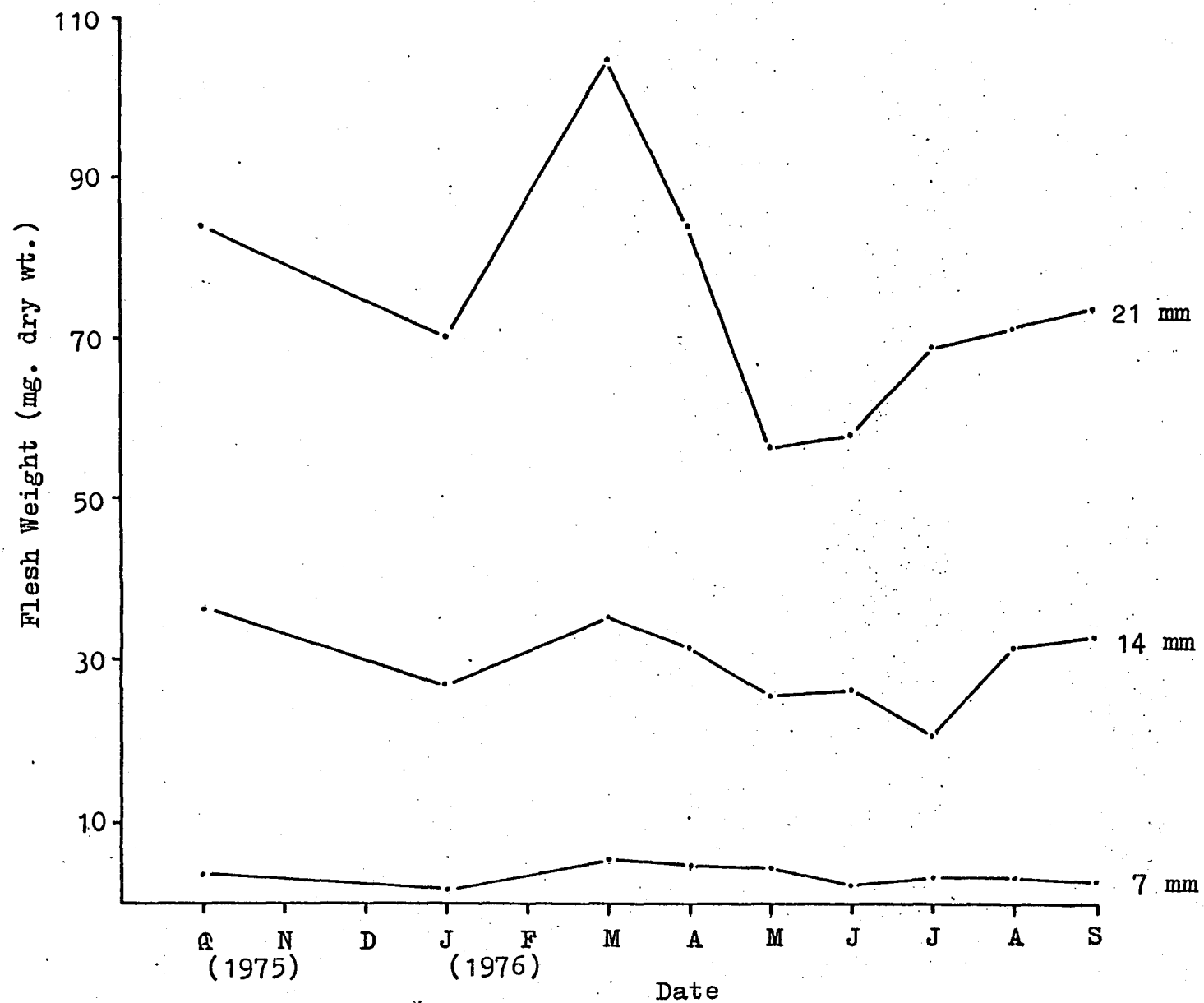


Figure 17. Regression of shell height and length
for Protothaca staminea.

